1   Short title: Individuality in seabird migration

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3   **Individual consistency in migratory behaviour of a pelagic seabird**

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Abstract

Many animals migrate between breeding and wintering areas; however, whether each animal behaves consistently in space and time between consecutive years is less well understood. Furthermore, previous breeding state (successful or failed) is often not considered when attempting to understand consistent individual differences in behaviour that are likely to impact upon the subsequent behaviour. Between 2006 and 2010, we used geolocators to track the migratory movements of a pelagic seabird, the streaked shearwater *Calonectris leucomelas*, with individuals ($N = 46$) being followed for two years or more, including 23 birds that had chicks in two seasons and 23 birds in just one season. All individuals, except for one bird, migrated to the same broad wintering areas, and their migratory route as well as the centre of wintering distribution did not change in relation to the previous breeding outcomes. Migration schedules (dates of departure from the breeding colony, southward and northward migrations, and first return to the colony) did not differ significantly between years for individuals that had chicks during both years, while failed individuals left the breeding colony and appeared to start the southward migration at an earlier date than the previous successful year. Nonetheless, the timing of the southward migration was consistent within individuals, including both males and females, over successive years regardless of the previous breeding outcome, and also the timing of first return back to the colony for females that had chicks in the both previous years and eggs in the both following season. This may imply the existence of individual-specific broad time schedules, possibly a circannual rhythm, though ecological conditions might affect the exact timing of the

45 actual departure event. Our results present evidence for high levels of individually

46 consistent behaviour for this pelagic seabird outside the breeding season.

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51 **1. Introduction**

52 Within the field of animal behaviour, there is a growing interest in identifying

53 individual differences within a population (Bolnick et al., 2003; Austin et al., 2004).

54 Until recently, conspecific individuals have been treated as ecologically equivalent, and

55 population averages have been considered to be sufficient for understanding a species

56 ecological dynamics. However, different individuals may use different resources, even

57 within the same population and species (Bolnick et al., 2003). Therefore,

58 acknowledging individual differences may have potentially profound implications for

59 understanding ecological and evolutionary processes, and indeed conservation

60 objectives and implementation programs (Dingemanse & Réale, 2005; Schofield et al.,

61 2010).

62   In contrast to activities observed during the breeding season, individual

63 behavioural differences and its repeatability outside the breeding season are less well

64 documented (reviewed in Bell et al., 2009). Many animals often migrate for more than

65 several hundred kilometers between breeding and wintering areas during the

66 non-breeding period (Le Boeuf et al., 2000; Phillips et al., 2005; Broderick et al., 2007;

67 Alerstam et al., 2006; Stanley et al., 2012). During this period, individual differences in

68 behaviour (in terms of space and time) within a population and consistency within

69 individuals between consecutive years have been rarely examined due to our inability of

70 following specific animals. This is also true for avian species, even though bird

71 migration has been relatively well studied (Newton, 2008). Spatial and temporal

72 repeatability estimates of migratory birds have been based on observations and

73 recaptures of marked individuals at breeding, wintering, or stopover locations (Møller,

74 2001; Catry et al., 2004; Battley, 2006), and also examined using the stable isotope

75 method (Phillips et al., 2009; Quillfeldt et al., 2010). However, these studies only

76 provide snapshots about repeatability during migration. Also, although satellite-linked

77 tags (PTTs) provide accurate positions over a long time, they can be applied only to

78 relatively large-sized species (e.g. ospreys; Alerstam et al., 2006) due to the size and

79 weight. In addition, recent studies suggest that breeding performance is likely to impact

80 upon the subsequent wintering ecology (and *vice versa*) (so-called 'carry-over effect';

81 reviewed by Harrison et al., 2010). However, previous studies often did not consider the

82 breeding outcome for understanding consistent individual differences in behaviour (but

83 see Phillips et al., 2005; Catry et al., 2013).

84 Streaked shearwaters *Calonectris leucomelas* are a pelagic seabird, that breed

85 in southeast Asia (Oka, 2004). Our previous study examined the migratory behaviour of

86 streaked shearwaters using light-based geolocators, and showed three distinct wintering

87 areas during non-breeding period: the seas off northern New Guinea, Arafura Sea, and

88 South China Sea (Yamamoto et al., 2010). Streaked shearwaters exhibited large

89 variation in the timing of southward migration between individuals (more than 3 months

90 between the first and last birds) (Yamamoto et al., 2010). Consequently, these results

91 give rise to a question as to whether each individual migrates to the same wintering

92 areas with a fixed migratory schedule between consecutive years. Furthermore, we may

93 expect changes in the subsequent wintering behaviour in relation to prior breeding

94 performance; our previous study examined the migratory behaviour of this species only

95 for one season (Yamamoto et al., 2010). Variation in the wintering destination (3

96 choices) and timing of migration (over 3 months) among a population of streaked

97 shearwaters may provide us with an opportunity to examine repeatability or plasticity in

98 behaviour of individuals outside the breeding season over different years.

99 Between 2006 and 2010, we used geolocators to track the migratory

100 movements of streaked shearwaters, with individuals ($N = 46$; 25 males and 21 females)

101 tracked for two years or more, each with known breeding status. The aims of our study

102 were to examine the variation between individuals and levels of individual consistency

103 in migratory behaviour outside breeding season, including their fidelity to certain

104 wintering areas, migratory routes, and repeatability in migratory schedules over years in

105 relation to their sex and breeding outcomes.

106

107 **2. Material and methods**

108 *2.1. Bird Tracking*

109 Fieldwork was carried out at the breeding colonies on Sangan Island (39°18'N,

110 141°58'E), Mikura Island (33°52'N, 139°14'E) and Awa Island (38°27'N, 139°13'E) in

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111 Japan. In streaked shearwaters, arrival at the breeding colony takes place mostly in

112 March, laying occurs from late June to early July, hatching in mid-August, and fledging

113 in mid-November (Oka et al., 2002; Yamamoto et al., 2010, 2012). Only one egg is laid

114 per breeding attempt and there are no replacement clutches. Over a five year period

115 from 2006 to 2010, we hand-captured 100 streaked shearwaters (different individuals)

116 nesting in burrows during the chick-rearing period from late August to late September,

117 and fitted geolocators (Mk4: 25 x 18 x 7 mm, 4.5 g or Mk5: 18 x 18 x 6.5 mm, 3.6 g,

118 developed by the British Antarctic Survey, Cambridge, UK) to the tarsus of each bird

119 using a plastic leg ring (see Figure 1 in Takahashi et al., 2008) (Table 1). All birds were

120 rearing their single chicks at the time of geolocator attachment; individuals with chicks

121 were targeted in this first year to ensure they were breeding birds and not simply

122 prospecting birds that may eventually breed elsewhere. In total, we recaptured 75

123 equipped birds from the respective breeding colonies one year after the attachment

124 during the incubation (from early to mid-August) or chick-rearing (from mid-August to

125 late September). All devices were removed, with new geolocators being attached to 51

126 recaptured birds for a second year of tracking, of which we recaptured and removed

127 devices from 42 birds the following season during the incubation (from early to

128 mid-August) or chick-rearing (from mid-August to late September). For a consecutive

129 year of tracking, we reattached geolocators to the recaptured birds, including some

130 individuals that did not have eggs and/or some failed to hatch eggs. In the second year,

131 23 birds (12 males and 11 females) had chicks, but 23 (13 males and 10 females) did not.

132 Note that we recaptured one bird from Sangan Island equipped in 2006 after three years,

133   and three birds from Mikura Island equipped in 2006 and two birds from Awa Island

134   equipped in 2008 after two years since the first year of geolocator attachment (Table 1).

135   Also, one bird from Sangan Island tracked for the second year with a new geolocator in

136   2007 was recaptured during the chick-rearing period after two years since the

137   deployment, obtaining three consecutive year tracking data (please see Table 1 for the

138   details of GLS attachment/recovery numbers). Two loggers (one from Sangan bird and

139   one from Awa bird) had recording errors, and the data were unusable. Consequently, 30

140   birds at Sangan Island ($N = 27$ in 2006-2008, $N = 3$ in 2007-2009), four birds at Mikura

141   Island ($N = 4$ in 2006-2008), and 10 birds at Awa Island ($N = 10$ in 2008-2010) were

142   tracked during two consecutive years, and two birds at Sangan Island were tracked for

143   three consecutive years (2006-2009) (46 birds in total, with 25 males and 21 females).

144   The sex of all the birds was determined based on their vocalizations during handling, as

145   the calls of males are high pitched whereas those of females are low pitched (Arima &

146   Sugawa, 2004).

147   We monitored chicks of the equipped birds during the chick-rearing period,

148   and determined the breeding outcome (success or failure) of the birds by direct

149   observation of their chicks on the last date of monitoring (usually in the mid-October),

150   as streaked shearwaters raise their chick until early November (Oka et al., 2002). Also,

151   we determined the breeding status (the existence of an egg) of the birds by examining

152   whether the geolocator data included repeated periods of darkness, assumed to represent

153   time spent within the nest burrow during incubation (Yamamoto et al., 2012).

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154   During the deployment/recovery, birds were handled for less than 8 min, and

155   immediately released to their nests after handling. The total mass of the geolocator with

156   the plastic leg ring was 7 g (Mk4) and 6 g (Mk5), which represents about 1.2% of the

157   mean body mass of the birds (mean ± SD = 576 ± 73 g, N = 100) and ca. 1.6% of the

158   body mass of the smallest bird (435 g). Upon recovery, we removed the logger and

159   plastic leg ring from each individual. We did not observe any injuries to their legs.

160

161   *2.2 Data Analysis*

162   Geolocators measure light levels at 60 s intervals, and record the maximum value

163   during each 10 min period. Immersion in seawater was measured every 3 s and

164   compiled over each 10 min period. Water temperature was recorded every 10 min only

165   after continuous immersion for 20 min. Light data were processed following the

166   procedures in Takahashi et al. (2008) and Yamamoto et al. (2010). Day length is used to

167   provide an estimate of latitude, while the relative timing of recorded midday or

168   midnight is used to provide an estimate of longitude (Hill, 1994).

169   We identified the date of final departure and first return to the breeding colony

170   before and after the migration, respectively, using light and immersion data (Yamamoto

171   et al., 2010). Because streaked shearwaters land at the breeding colony after dusk, and

172   depart the colony before dawn, immersion data were recorded as 0 (out of water) over

173   the substantial period of the night that birds were at the colony. We assumed that birds

174   were migrating south when they crossed a boundary 500 km south or west of the

175   breeding colony (Yamamoto et al., 2010). Also, we assumed that birds had reached their

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176 final wintering destinations after crossing one of three predetermined boundaries (10°N

177 for the seas off northern New Guinea, the Equator for the Arafura Sea, and 120°E for

178 the South China Sea), as defined in Yamamoto et al. (2010). Similarly, we assumed that

179 birds were migrating north when they flew from one of the three predetermined

180 boundaries to within 500-km of the colony. Immersion data were partially or completely

181 unavailable for two birds, and, thereby, the dates of departure from the breeding colony

182 and/or first return to the colony were not obtained from these birds. In addition, one

183 logger stopped logging light intensity on 26 January 2007; therefore, the location data

184 for this bird were unavailable after that date. At-sea distributions of streaked

185 shearwaters during the post-breeding period were established by fixed kernel density

186 maps using the Spatial Analyst toolkit in ArcGIS 9.3 (ESRI®).

187 To inspect the variation in repeatability along the migratory route within

188 individuals, we calculated the mean value of longitude within each 5º interval of

189 latitude between 30ºN and 0º (e.g. for a bird migrated to the seas off northern New

190 Guinea, the mean value of longitude at latitudes of > 25º - < 30º, > 20º - < 25º, > 15º - <

191 20º, > 10º - < 15º, were calculated), and averaged. Then, we calculated the distance

192 between the migratory routes for two years. Similarly, we calculated the distance

193 between the centroids of wintering distribution for two years within the same

194 individuals.

195 Statistical analyses were performed in R software, version 2.5.1 (R

196 Development Core Team). Because we conducted the study at three different breeding

197 colonies over a five-year period from 2006 to 2010, possible colony and year effects on

198 the dependent variables (i.e. migratory schedules) were tested by including those as

199 predictors in generalized linear models (GLM) with breeding status as an independent

200 variable. Colony and year never proved to be significant predictors of the dependent

201 variables, and, thus, we did not consider colony and year effects in our analysis.

202 Although annual conditions in the marine environment (e.g. sea surface temperatures)

203 appear to influence the timing of migration for several marine vertebrates (e.g.

204 Sherrill-Mix et al., 2008), breeding outcome and endogenous rhythm probably more

205 significantly influence the broad timing of movement (see Discussion). Also, colony

206 differences, if there is, are probably less apparent due to different sample sizes between

207 the colonies (30 birds at Sangan Island, four birds at Mikura Island, and 10 birds at Awa

208 Island). Effects of the sex and previous breeding outcome on the consistency in

209 migratory route and wintering distribution are examined using GLM. Timings of each

210 migratory event of the same individual between two years were compared using paired

211 t-test. Repeatability in an individual's migratory schedule between years was evaluated

212 using the intraclass correlation coefficient (r) (Zar, 1999). Values are presented as mean

213 ± SD; p values < 0.05 were considered significant.

214

3. Results

3.1 Spatial Consistency

217 Streaked shearwaters migrated to three distinct wintering areas during the post-breeding

218 period: the seas off northern New Guinea, Arafura Sea, and South China Sea (Figure 1).

219 Of the 46 individuals, 45 migrated to the same wintering areas over the two years

220   (Figure 2a, c, d, e). Furthermore, two individuals also migrated to the same wintering

221   area for three successive years (Figure 2b). Only one individual (male) changed its

222   wintering destination over two years from the Arafura Sea to seas off northern New

223   Guinea (with 1303 km separation between the centroids of the two wintering areas)

224   (Figure 2f). In birds exhibiting fidelity to wintering areas, the mean distance between

225   the centroids of the wintering area for two years within the same individuals was 459 ±

226   326 km in males and 259 ± 204 km in females. There was no difference in the distance

227   between the centroids of the wintering area for two years depending on the previous

228   breeding outcomes (success or failure), but males showed larger distances compared to

229   females (GLM, breeding outcome: $t = -1.28$, $p = 0.21$, sex: $t = 2.47$, $p < 0.05$).

230   Individuals followed similar migratory routes between years (Figure 2a-e).

231   The distance between migratory routes for two years within individuals was 299 ± 138

232   km in males and 252 ± 177 km in females for the southward migration as well as 551 ±

233   341 km in males and 452 ± 354 km in females for the northward migration. There was

234   no difference in the distance between migratory routes for two years in relation to the

235   sex and previous breeding outcome (GLM, all $p > 0.30$). Furthermore, streaked

236   shearwaters from Awa Island appeared to show two different migratory routes when

237   leaving or when approaching Japan (through the Pacific Ocean, $N = 8$, vs. through the

238   Sea of Japan, $N = 2$; Figure 2c, d, respectively); all individuals took the same route as in

239   the previous year.

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241   *3.2. Temporal Consistency*

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242   Migration schedules (dates of departure from the breeding colony, southward and

243   northward migrations, and first return to the colony) did not differ between years for

244   individuals that had chicks during both years (paired t-test, all $p > 0.15$ for both males

245   and females). On the other hand, individuals that did not have chicks in the second year

246   left the breeding colony significantly earlier (paired t-test, male: $t_{13} = 3.88$, $p < 0.01$,

247   female: $t_{10} = 2.69$, $p < 0.05$) (Figure 3a), and males started the southward migration at

248   an earlier date ($t_{13} = 3.07$, $p < 0.05$) than the previous successful year (ca. 12 days

249   earlier) (Figure 3b). Females also started the southward migration slightly earlier (ca. 3

250   days earlier) than the previous year, though it was not significant ($t_{10} = 0.92$, $p = 0.38$).

251   For these birds, the timing of northward migration and first return to the colony did not

252   significantly differ between previously successful and failed years (northward

253   migration: $t_{13} = -1.47$, $p = 0.17$ for male and $t_{10} = 1.12$, $p = 0.29$ for female; first return:

254    $t_{13} = -1.18$, $p = 0.26$ for male and $t_{10} = 1.03$, $p = 0.33$ for female). Meanwhile, we found

255   a significant between-year individual consistency in the timing of southward migration

256   regardless of the previous breeding outcome (Figure 3b), and also for the first return

257   back to the colony in females that had chicks for the both previous years (Figure 3d).

258   There was no repeatability within individuals in the timing of departure from the colony

259   and northward migration for both groups (Figure 3a, c).

260   The timing of first return back at the breeding colony was unrelated to the

261   subsequent breeding outcome (i.e. whether individuals had eggs in the following

262   season) (paired t-test: all $p > 0.13$ for both males and females). Also, there was no

263   repeatability within individuals in the timing of first return for these groups

264   (repeatability test: all $p > 0.07$), except for females that had eggs in the both following

265   season ($r = 0.59, p < 0.05$).

266

267   **4. Discussion**

268   The key finding from our study was to reveal the individual consistency in spatial and

269   temporal migratory pattern of a pelagic seabird, and its relation with the breeding

270   outcome before and after the migration, using robust sample sizes ($N = 46$). Recently,

271   using electronic tags, individual consistency in behaviour outside the breeding season,

272   including site fidelity and consistency in the chronology of movement, has been

273   reported for a variety of terrestrial and marine taxa (Bradshaw et al., 2004; Phillips et al.,

274   2005; Broderick et al., 2007; Jorgensen et al., 2010; Schofield et al., 2010; Vardanis et

275   al., 2011; Stanley et al., 2012), while some animals also exhibit a level of plasticity

276   (Dias et al., 2011; Guilford et al., 2011). Nonetheless, the number of individuals tracked

277   for more than one year is usually small. Although Bogdanova et al. (2011) showed the

278   differences in winter distribution in relation to the prior breeding outcome, they were

279   unable to present results for the same individuals with a different breeding status

280   (success vs. failure). Only a few studies examined the individual consistency in

281   migratory behaviour in relation to the breeding outcome (Phillips et al., 2005; Catry et

282   al., 2013).

283   Our study provides strong evidence for high levels of individually consistent

284   behaviour for a pelagic seabird migrating within the western Pacific Ocean. Streaked

285   shearwaters showed a high degree of consistency in their wintering area over years.

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286 Furthermore, each individual exhibited fidelity to relatively small-scale areas within the

287 broad wintering areas, and their wintering distributions did not change in relation to the

288 prior breeding outcomes. Recent studies suggest that the fidelity to a specific wintering

289 site is relatively common characteristic among migratory animals (e.g. Bradshaw et al.,

290 2004; Phillips et al., 2005; Broderick et al., 2007). However, one out of 46 streaked

291 shearwaters tracked changed the wintering area in the subsequent year in our study,

292 assuming their possible flexibility in migratory behaviour. A previous study suggested

293 that Cory's shearwaters *Calonectris diomedea*, a closely related species to streaked

294 shearwaters, have several potential wintering areas, and some individuals (36% of study

295 birds) within a population changed the wintering destination between years (Dias et al.,

296 2011). Similarly, streaked shearwaters could change their wintering destination in any

297 given year, but individuals did not or might be unlikely to migrate to different wintering

298 areas over consecutive years. One possibility could be that individuals benefit from

299 multiyear site fidelity to specific foraging areas, as it provides for increased familiarity

300 with local resources (Bradshaw et al., 2004; Newton, 2008). Also, streaked shearwaters

301 wintered in tropical oceans where annual fluctuation of marine environment is usually

302 less pronounced (i.e. predictable) (Longhurst & Pauly 1998), and, therefore, flexibility

303 would be less advantageous for them compared to species exploits a highly

304 unpredictable environment (Quillfeldt et al. 2010). On the other hand, males showed

305 relatively larger differences in the wintering distribution between two years compared to

306 females. Although the reason of this sex-related difference is unknown, there is a

307 possibility that males are more likely to exploit large areas, as one individual that

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308   changed its wintering destination in our study was also male.

309   Individuals migrated along similar pathways within a few hundred kilometers

310   between the breeding colony and wintering area, and the migratory route did not differ

311   between two years depending on the breeding outcome and sex; though the precision of

312   light-level based geolocation data in estimating location is low (± 186 km; Phillips et al.,

313   2004). This is probably also supported, in part, by the result from individuals from Awa

314   Island that showed two different migratory routes from the breeding colony to the

315   wintering areas (Pacific vs. Japan Sea), and each individual migrated along the same

316   route over two years. The distance between migratory routes for two years was

317   relatively larger during the northward migration, probably because the low accuracy in

318   estimating positions around the spring equinox when most shearwaters were migrating

319   towards the breeding colony from the wintering area. Similarly, route fidelity has been

320   noted in several species (Le Boeuf et al., 2000; Broderick et al., 2007), but also

321   flexibility in route in terrestrial and marine environment (Alerstam et al., 2006;

322   Schofield et al., 2010; Guilford et al., 2011; Vardanis et al., 2011; Stanley et al., 2012).

323   Route fidelity may be affected by conditions en route that are likely to change between

324   years and regions (Bauer et al., 2010), or possibly related to migratory strategy

325   (heritability vs. learning).

326   Previous studies have reported that failed breeders start their outward

327   migration earlier than do successful breeders (Phillips et al., 2005; Bogdanova et al.,

328   2011; Catry et al., 2013), because the timing of departure from the colony is probably

329   constrained by the condition and/or age of their chicks in a given year. Our results

330　support this; individual streaked shearwaters that did not have chicks in the second year

331　of our study left the breeding colony earlier and appeared to start their southward

332　migration overall earlier than in the previous year when they successfully fledged

333　offspring. Nonetheless, individuals, including males and females, exhibited repeatability

334　in the timing of their southward migration regardless of the previous breeding outcome,

335　with a great variation in the timing between individuals (8 October–15 January). This

336　may imply that individual streaked shearwaters have specific time schedules for the

337　timing of their migration, possibly a circannual rhythm (Gwinner, 1996; Newton, 2008).

338　Meanwhile, such an endogenous rhythm could only initiate the preparatory processes,

339　and at a particular date, weather, food, and other ecological conditions might then play

340　an important role in altering the exact timing of the actual departure event (Bradshaw &

341　Holzapfel, 2007; Newton, 2008), resulting in an overall earlier southward migration in

342　failed birds.

343　　　We found no repeatability within individuals for the timing of northward

344　migration. Endogenous rhythms could drift under the conditions of constant daylength

345　in the tropical region (Bradshaw & Holzapfel, 2007; Newton, 2008) where shearwaters

346　spent the post-breeding period. Birds possibly use other photic cues (e.g. light intensity

347　fluctuation) as found in some tropical birds (Newton, 2008; Goymann et al., 2012),

348　though these are relatively weak compared with the photoperiodic cues (Goymann et al.,

349　2012). Also, as repeatability is a measure of individual consistency relative to other

350　individuals in the population, the repeatability was less detectable for the timings of

351　northward migration due to less variability between individuals (13 February–18

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352   March) compared to that for the southward migration, ranged over three months.

353   Females that had chicks in the both previous years exhibited repeatability in the timing

354   of first return back to the breeding colony, while successful males and failed individuals

355   did not. In closely-related Cory's shearwaters, failed birds depart earlier from wintering

356   areas and arrived sooner at the breeding colony, probably because they would be in a

357   more favorable state due to their reduced parental investment during the previous

358   breeding period (Catry et al., 2013). In this study, the timing of northward migration and

359   first return to the colony did not differ between years depending on the previous

360   breeding state (success or failure). Hence, in this respect, the previous breeding state (i.e.

361   parental investment) is less likely to carry over to the subsequent behaviour during the

362   non-breeding period in streaked shearwaters. However, as females that had chicks in the

363   both previous years and that had eggs in the both following season exhibited the

364   repeatability, the breeding state may affect the time schedule within individuals for first

365   return to the colony and *vice versa* in females, possibly related to their body condition.

366   In males, there was no repeatability in the timing of first return to the colony regardless

367   of the any breeding state. Although the timing of first return to the breeding colony is

368   likely to be an important consequence for breeding attempt, such as nest occupation and

369   reunion of pairs (Kokko, 1999; Gunnarsson et al., 2004), it was not related to the

370   subsequent breeding outcome in males. Streaked shearwaters show a long period of

371   pre-laying (ca. three months), and, during this period, males return to the breeding

372   colony probably to defend their nests from other prospecting birds (Yamamoto et al.,

373   2011). Therefore, activities during the pre-laying period may be more critical for

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374   reproductive success in males.

375   Recent climate-related changes undoubtedly appear to affect behaviour and

376   phenology of a variety of taxa during both breeding and non-breeding period (review by

377   Walther et al., 2002, Austin & Rehfisch, 2005). Under such situations, plasticity in

378   behaviour would represent an adaptive advantage (Parmesan, 2006, Reed et al., 2010).

379   Individual consistency in behaviour exhibited in streaked shearwaters is possibly

380   disadvantageous for responding to a changing environment. Nonetheless, on the other

381   hand, individual differences in behaviour within a population would allow a certain

382   individuals to cope with such changes (Ghalambor et al., 2007). Also, individual

383   differences in behaviour are considered to occur through time and across situations

384   (Bolnick et al., 2003; Bell et al., 2009), assuming that behaviour during the

385   non-breeding period is also likely to affect, to some extent, behaviour during the

386   breeding period, and *vice versa*. Examining individual behaviour over the entire annual

387   cycle may therefore provide us with a prime opportunity to understand how individual

388   differences in behaviour shape life history traits and to relate this to fitness.

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531

Figure legends

532 **Figure legends**

533 Figure 1. Wintering distribution of streaked shearwaters (95% kernel density maps for

534 each wintering area: the seas off northern New Guinea, Arafura Sea, and South China

535 Sea). Stars indicate the colony location (Sangan, Awa, and Mikura Islands).

536

537 Figure 2. Example migration tracks for individual streaked shearwaters in successive

538 years. Stars indicate the breeding colony (Sangan, Awa, and Mikura Islands). Red lines

539 represent the migration pathway in the first year, blue lines in the second year, and

540 green line in the third year. Panels (a, c, d, e) show examples of individuals that were

541 faithful to their wintering areas for two successive years, or (b) for three successive

542 years. Birds migrated to (b, e) the seas off northern New Guinea, (a) the South China

543 Sea, and (c, d) the Arafura Sea. In addition, birds from Awa Island exhibited two

544 different migratory routes: (c) a route through the Pacific Ocean, and (d) through the

545 Sea of Japan. Panel (f) shows the migration track of the only bird that changed its

546 wintering destination in the successive year.

547

548 Figure 3. Repeatability for timings in the migration schedule between two years: (a)

549 departure from the breeding colony, (b) southward migration, (c) northward migration,

550 (d) first return at the breeding colony. White thick and thin circles represent males and

551 females that had chicks in both previous seasons (BB), while black and grey circles

552 represent males and females with no chick in the second previous season (BF),

553 respectively. Statistical results for the repeatability (r) are shown.

26

Table 1. Number of geolocator attachment and recovery.

Colony	Year (attach-recover/attch-recover)	No. of 1st-year GLS Attachment	No. of 1st-year GLS Recovery	No. of 2nd-year GLS Attachment	No. of 2nd-year GLS Recovery
Sangan Island	2006-2007-2008	48 (24 males, 24 females)	39[a] (21 males, 18 females)	35 (19 males, 16 females)	29[b] (15 males, 14 females)
	2007-2008-2009	14 (7 males, 7 females)	14 (7 males, 7 females)	4 (2 males, 2 females)	3 (1 male, 2 females)
Mikura Island	2006-2007-2008	16 (7 males, 9 females)	10[c] (6 males, 4 females)	1 (1 female)	1 (1 female)
Awa Island	2008-2009-2010	22 (14 males, 8 females)	18[d] (12 males, 6 female)	11 (6 males, 5 females)	9 (4 males, 5 females)

[a]including 1 recovered after 3 years (1 male).
[b]including 1 recovered after 2 years (1 male).
[c]including 3 recovered after 2 years (2 males, 1 female).
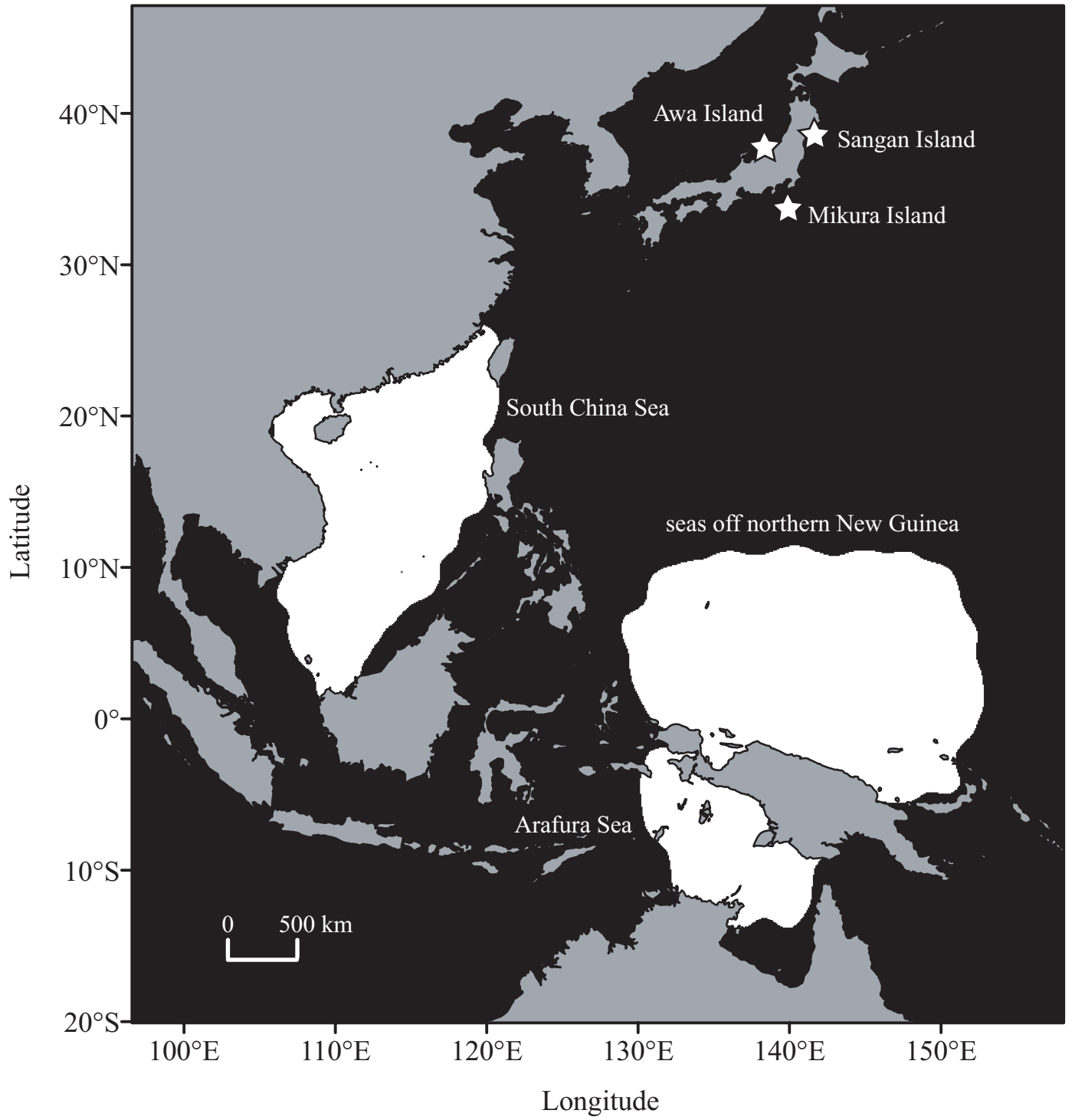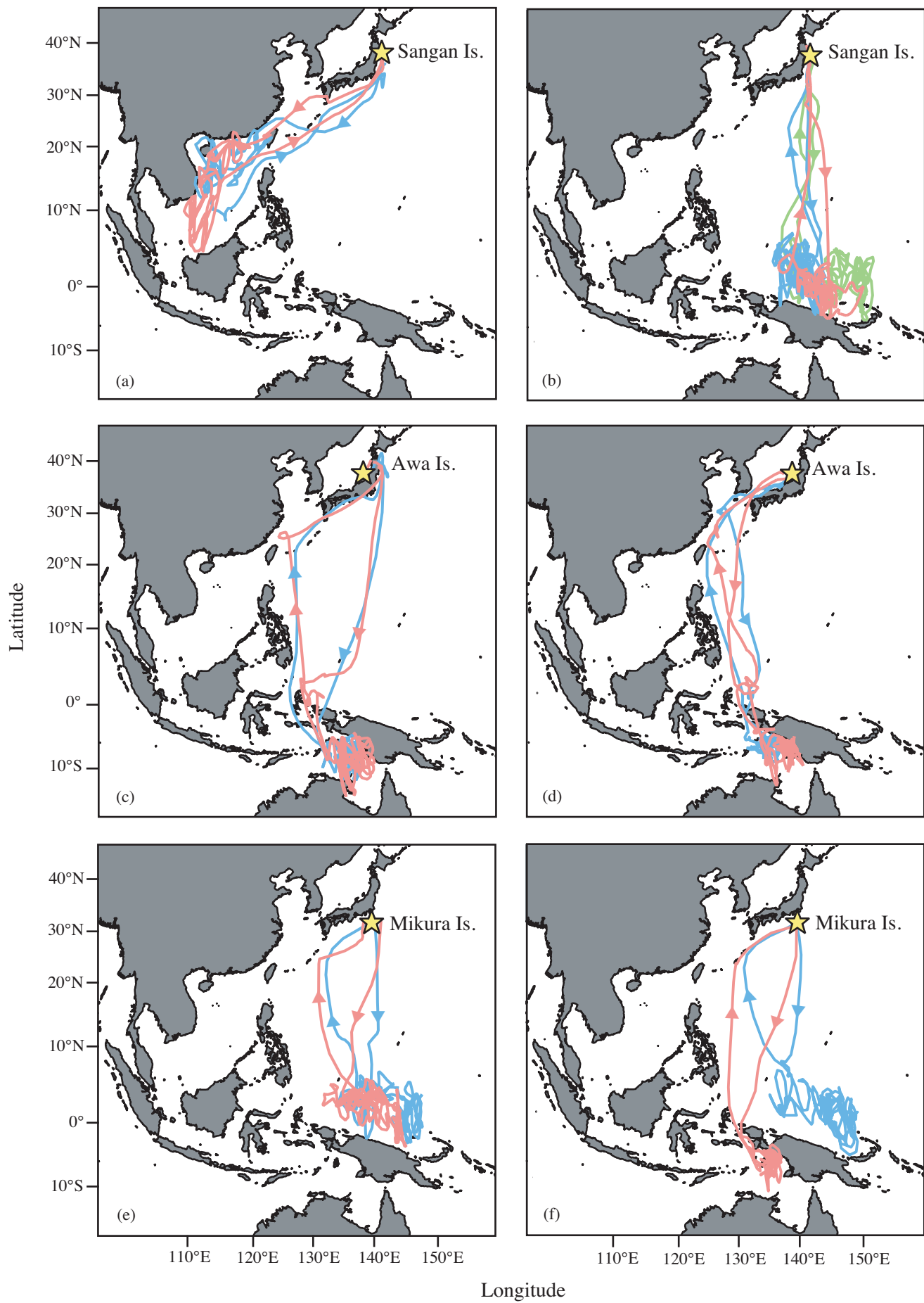[d]including 2 recovered after 2 years (2 males).
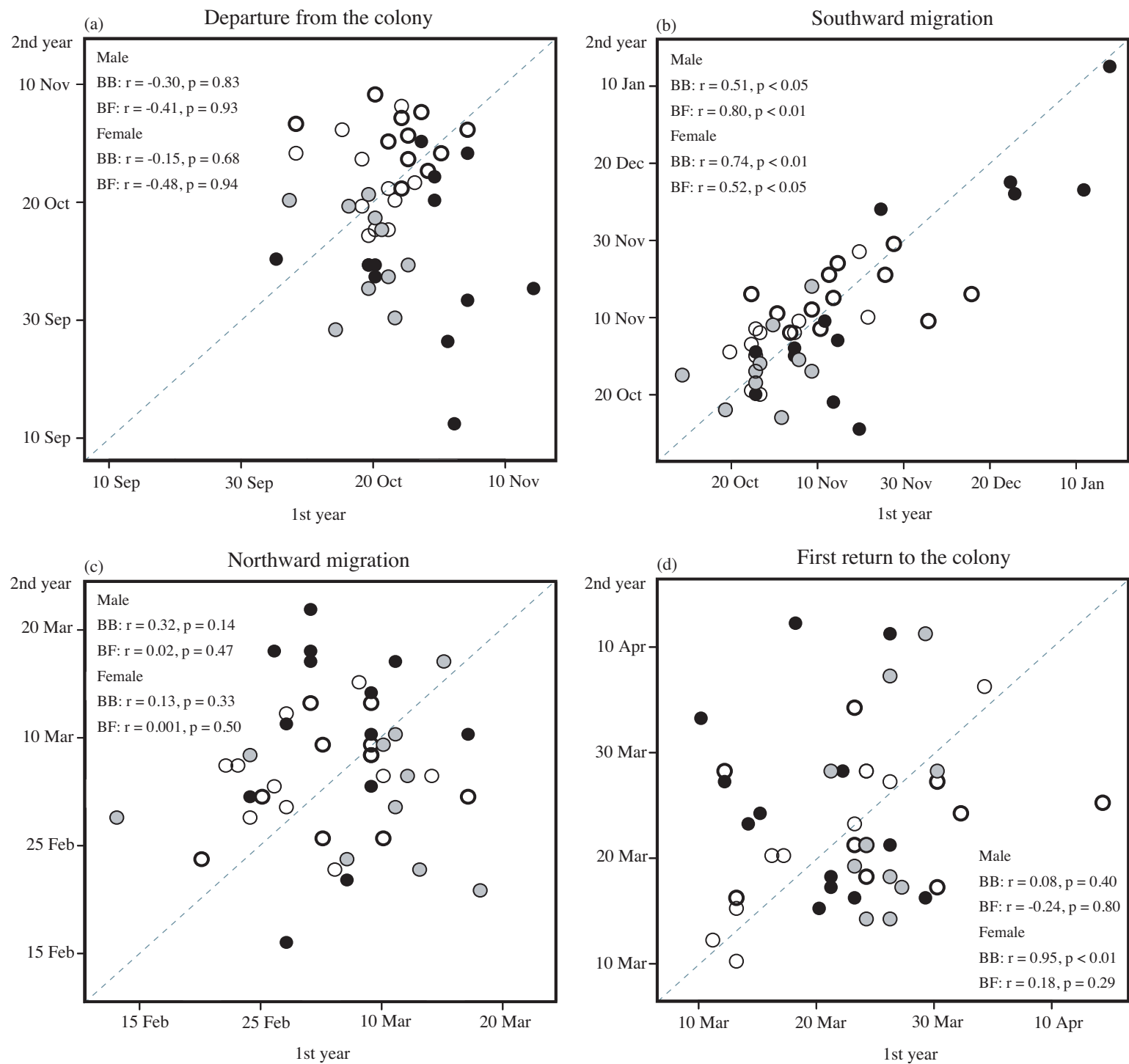
Figure 1

Figure

Figure 2

Figure

(a) Departure from the colony

2nd year axis: 10 Nov, 20 Oct, 30 Sep, 10 Sep
1st year axis: 10 Sep, 30 Sep, 20 Oct, 10 Nov

Male
BB: r = -0.30, p = 0.83
BF: r = -0.41, p = 0.93
Female
BB: r = -0.15, p = 0.68
BF: r = -0.48, p = 0.94

(b) Southward migration

2nd year axis: 10 Jan, 20 Dec, 30 Nov, 10 Nov, 20 Oct
1st year axis: 20 Oct, 10 Nov, 30 Nov, 20 Dec, 10 Jan

Male
BB: r = 0.51, p < 0.05
BF: r = 0.80, p < 0.01
Female
BB: r = 0.74, p < 0.01
BF: r = 0.52, p < 0.05

(c) Northward migration

2nd year axis: 20 Mar, 10 Mar, 25 Feb, 15 Feb
1st year axis: 15 Feb, 25 Feb, 10 Mar, 20 Mar

Male
BB: r = 0.32, p = 0.14
BF: r = 0.02, p = 0.47
Female
BB: r = 0.13, p = 0.33
BF: r = 0.001, p = 0.50

(d) First return to the colony

2nd year axis: 10 Apr, 30 Mar, 20 Mar, 10 Mar
1st year axis: 10 Mar, 20 Mar, 30 Mar, 10 Apr

Male
BB: r = 0.08, p = 0.40
BF: r = -0.24, p = 0.80
Female
BB: r = 0.95, p < 0.01
BF: r = 0.18, p = 0.29

Figure 3